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Review

# Pursuing the Potential of Heirloom Cultivars to Improve Adaptation, Nutritional, and Culinary Features of Food Crops

**Sangam Dwivedi [1], Irwin Goldman [2] and Rodomiro Ortiz [3,*]**

[1] Independent Researcher, Hyderabad, Telangana 500001, India
[2] Department of Horticulture, College of Agricultural and Life Sciences, University of Wisconsin Madison, 1575 Linden Drive, Madison, WI 53706, USA
[3] Department of Plant Breeding, Swedish University of Agricultural Sciences, Sundsvagen 10 Box 101, SE 23053 Alnarp, Sweden
* Correspondence: rodomiro.ortiz@slu.se; Tel.: +46-4041-5527

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**Abstract:** The burdens of malnutrition, protein and micronutrient deficiency, and obesity cause enormous costs to society. Crop nutritional quality has been compromised by the emphasis on edible yield and through the loss of biodiversity due to the introduction of high-yielding, uniform cultivars. Heirloom crop cultivars are traditional cultivars that have been grown for a long time (>50 years), and that have a heritage that has been preserved by regional, ethnic, or family groups. Heirlooms are recognized for their unique appearance, names, uses, and historical significance. They are gaining in popularity because of their unique flavors and cultural significance to local cuisine, and their role in sustainable food production for small-scale farmers. As a contrast to modern cultivars, heirlooms may offer a welcome alternative in certain markets. Recently, market channels have emerged for heirloom cultivars in the form of farmer–breeder–chef collaborations and seed-saver organizations. There is therefore an urgent need to know more about the traits available in heirloom cultivars, particularly for productivity, stress tolerance, proximate composition, sensory quality, and flavor. This information is scattered, and the intention of this review is to document some of the unique characteristics of heirloom cultivars that may be channeled into breeding programs for developing locally adapted, high-value cultivars.

**Keywords:** consumer-oriented breeding; consumer-oriented germplasm conservation; culinary; farmer–breeder–chef–consumer nexus; genetic diversity; heritage seedbank; local food systems; seed-savers; stress tolerance

## 1. History and Survival of Heirloom or Folk Cultivars

Heirloom cultivars are characterized as traditional or older cultivars that are open-pollinated, passed down from gardener to gardener or handed down in families, and often not used in large-scale agricultural enterprises. The definition of heirloom varies, and the term itself does not carry precise scientific designations. One of the most typical concepts of an heirloom is its non-hybrid, or open-pollinated nature. Heirlooms can be from cross- or self-pollinated species, but if the crop species is cross-pollinated, then the heirloom is considered open-pollinated. Because of this fact, some heirloom cultivars may be quite variable, and it is therefore apparent why heirlooms may not fit well into modern agricultural systems that place great value on uniformity. Votava and Bosland [1] found that the pepper cultivar 'California Wonder' had substantial amounts of genetic variability compared to a standard modern cultivar. They recommended that this cultivar not be used for genetic analysis because of this variability. In many cases, heirloom cultivars are known to possess more inherent variation than modern cultivars. Some of this variation could be due to their open-pollinated nature, and some might be due to the fact that they are often associated with seed-saving. The appearance of $F_1$ hybrids during the 20th century was arguably a tremendous advance in terms of crop productivity and seed commercialization. Some advocates of heirloom cultivars may, however, view the advance of $F_1$ hybrids as an incursion on traditional cultivars, as they rapidly usurped the use of traditional, open-pollinated cultivars for crop production purposes. While open-pollinated cultivars became a source for extracting the inbred lines that became parents of $F_1$ hybrid cultivars [2], the populations themselves were often not maintained or advanced as they once had been.

As $F_1$ hybrid cultivars became more common, gardeners and farmers began to notice the disappearance of heirloom or traditional cultivars. Importantly, many plant breeders and seed companies have invested their time and resources in hybrid cultivars for decades, thereby leaving heirloom, open-pollinated cultivars with a lower commercial status. In some parts of Europe, laws were passed that made it illegal to sell cultivars that were not on government-approved lists. Some of these laws also required substantial time and effort in the testing of cultivars before they could be listed. Part of the rationale was to ensure that cultivars were distinct, uniform, and stable, but many heirloom cultivars did not fit well into these criteria [3]. Thus, heirloom cultivars were, in some cases, relegated to the agricultural fringe [4].

Kingsbury [2] commented that at times of technological and social change, it is common to look back on simpler times. He suggests that the interest in heirloom cultivars may be due in part to this phenomenon, which idealizes the past. Another aspect of this yearning for simplicity is the fact that gardens represent, for some, a retreat from the stress of modernity. In this way, cultivating heirlooms may offer an opportunity for the gardener or eater to reconnect with a different age.

Additional aspects of the heirloom cultivar experience are the unique flavors and culinary qualities that generations of people had come to know and appreciate. Such qualities may be absent in modern cultivars bred for modern cropping systems, creating a desire for the heirloom. An example of such a quality is the creamy mouthfeel caused by high levels of water-soluble polysaccharides (also described as phytoglycogen) in heirloom sweet corn cultivars. The creamy mouthfeel caused by the polysaccharides was an important attribute of the *sugary-1* allele, which reduced starch accumulation in the maize endosperm and increased the amount of sugars [5]. As newer, sweeter $F_1$ hybrid cultivars were developed with the *shrunken-2* allele, the *sugary-1* allele was replaced. Cultivars homozygous for *shrunken-2* are noticeably sweeter than, perhaps even twice as sweet as those carrying *sugary-1*. However, they lack the creamy mouthfeel and some of the aromatics associated with older sweet corn cultivars [5]. Thus, an heirloom may deliver flavors and culinary qualities associated with specific, older cultivars and may thus represent an important aspect of heritage.

Heirloom cultivars also are associated with seed-saving, and, in fact, the generation-to-generation transfer of heirloom seed is often one of the defining features of an heirloom. Navazio [6] commented that the post-World-War-II era in the USA saw a major transition in agriculture, where more farmers were willing to purchase seed every season from seed companies. Prior to that time, farmers were involved heavily with producing their own seed, and with selecting and maintaining good seed stock. As farmers began purchasing seed annually from seed companies, heirloom cultivars and their systems of maintenance through seed-saving gradually diminished. Fortunately, a resurgence of interest in heirlooms has taken place in the last few decades. Several examples may illustrate this point. Today, some seed companies feature and celebrate heirloom cultivars in their catalogues. Gardeners and farmers regularly seek out, save, and preserve heirloom seed to continue the traditions of these unique cultivars, and consumers are willing to pay substantially more at the market for their products. The development of "new heirlooms" also is discussed in plant breeding fora, where the breeding program may begin with heirloom populations that are subject to selection for current conditions, but under the careful guidance of a seed-saver or local plant breeder. The Slow Food movement (https://www.slowfoodusa.org/) maintains a catalogue of heritage foods, including heirloom cultivars, run by the Ark of Taste (https://www.slowfoodusa.org/ark-of-taste). These foods, which include crop cultivars, are, according to Ark of Taste, "culturally or historically linked to a specified region, locality, ethnicity, or traditional production practice."

Heirloom cultivars are a part of the farming system in many regions of the world. For example, southern Appalachia is an area of high crop biodiversity in the USA, where many heirloom cultivars remain. Veteto [7] documented 134 heirloom cultivars that were still being grown in the region in a recent survey. He found that even though one or two individuals in a community were usually involved in maintaining significant numbers of heirloom cultivars, many communities had lost their heirloom vegetable cultivars. He found that the decline of the farming population and the lack of cultural continuance in family seed-saving traditions were likely responsible for this loss.

Among the problems associated with heirloom cultivars is their susceptibility to pathogens. In many cases, modern breeding has helped to improve host-plant resistance; thus, it is not surprising that heirloom cultivars may lack resistance to important pests. Heirloom tomato production can be limited by soilborne diseases such as bacterial wilt and fusarium, caused by the pathogens *Ralstonia solanacearum* and *Fusarium oxysporum* f.sp. *lycopersici*, respectively. A creative approach to this problem was discussed by Rivard and Louws [8], who grafted heirloom scions onto resistant rootstock. In naturally infested soil, bacterial wilt incidence for nongrafted 'German Johnson' was 79% and 75% over two years, but it had no symptoms of bacterial wilt if grafted onto the resistant genotypes CRA 66 or Hawaii 7996. Fusarium wilt incidence was 46% and 50%, respectively, in nongrafted and self-grafted German Johnson controls, but no symptoms of fusarium wilt were seen if plants were grafted onto resistant genotypes. Thus, grafting may be an appropriate approach for heirloom production in infected soils.

A debate is occurring as to whether modern cultivars are less nutritious than their heirloom counterparts. Barker et al. [9] examined differences in mineral nutrient concentrations between modern $F_1$ hybrids and heirloom cultivars of cabbage, and also looked at fertilization practices with either organic fertilizer and compost or conventional fertilizers. Crop production increased with conventional or organic fertilizers compared to compost. Mineral nutrient composition did not vary between modern or heirloom cultivars or among different fertility practices; however, the authors did find cultivar differences for nutrient concentration. The fact that mineral nutrient content did not vary between modern and heirloom cultivars is important in that it runs counter to popular press articles that suggest the nutritional quality of our food supply is decreasing. Flores et al. [10] examined carotenoid levels of traditional tomato cultivars. They found substantial amounts of variation for many carotenoids in colored fruit from these traditional cultivars, suggesting new opportunities for breeding. There is little doubt that heirloom cultivars contain reservoirs of useful traits, including those that might be able to contribute to improved human nutrition.

Van der Knaap and Tanksley [11] examined the genetic basis of the unique phenotype of the heirloom tomato cultivar 'Yellow Stuffer,' which looks more like a bell pepper than a traditional tomato. Their analysis was based on a segregating population derived from a cross between Yellow Stuffer and a wild species of tomato. They found three quantitative trait loci (QTL) that influenced fruit shape and seven QTL that influenced fruit mass, many of which had already been identified in other tomato mapping research. They were able to pinpoint an allele at *fs8.1* causing the convex locule walls that were responsible for the extended, bumpy shape of the pepper-shaped fruit in Yellow Stuffer. They surmised that the evolution of bell-pepper-shaped tomato fruit may have proceeded through mutations of some of the same genes that led to bell-pepper-type fruit in garden pepper.

Heirloom potatoes offer unique flavors and qualities that are sought after by consumers. Production of these heirloom types is, however, not well understood in the context of modern farming systems. Fandika et al. [12] investigated how irrigation and nitrogen management might be best employed in heirloom potatoes. They found that modern cultivars were more responsive to irrigation and nitrogen than heirloom potatoes. Interestingly, they found that higher applications of nitrogen decreased the yield of heirloom potato cultivars, whereas yields of modern cultivars were increased. Heirloom cultivars were more drought-tolerant, but required larger water inputs because of their later maturities.

Overall conclusions of this study suggested that production of heirloom types could be more expensive than that of modern cultivars.

Interest in seed-saving continues to grow in many parts of the developed world, perhaps as a response to the increasing consolidation of the global seed industry and a desire for more local control of plant genetic resources. Interest in heirloom cultivars goes hand in hand with this expanded interest in seed-saving. For the most part, these efforts are celebrated by communities who wish to build closer relationships with their seed sources. However, not everyone is celebrating. In the last five years, efforts have been made to close certain seed-lending libraries, which allow gardeners to check out packets of seed and return the seeds that they save from the crop grown. The cultivars made available by lending libraries are typically open-pollinated and often heirloom. Efforts to close lending libraries were based on an interpretation of the US federal Seed Act, which would have required seed-lending libraries to test seeds for germination and purity. In 2016, the state department of agriculture in Pennsylvania determined that such seed libraries are noncommercial seed exchanges and therefore not subject to the Seed Act. Additionally, a number of efforts have been initiated to resume breeding and seed-saving of open-pollinated cultivars. The Open Source Seed Initiative (www.osseeds.org), which started operations in 2014, is a clearinghouse for primarily open-pollinated cultivars that have been released into a "protected" commons. The protected nature of this commons means that anyone can breed with or save seeds of these open source cultivars, but cannot restrict others' use of them. Some of the cultivars contained in this registry include open-pollinated types, such as the new carrot cultivar "Dulcinea," that were bred recently to fill gaps in commercial seed company catalogs. Such open-pollinated types might be considered a modern spin on an heirloom cultivar.

Navazio [6] stated that the seed "is a reflection of the farming system as it is grown, cultivated, selected, and fully incorporated into that system." In this way, heirloom cultivars represent a farming system that considers and prizes traits of long-term interest to the farmer and consumer, the incorporation of seed-saving, family and community traditions, and the transference of plant genetic resources from generation to generation. Heirloom cultivars long cultivated locally by people around the world may be a critically important tool in creating a more sustainable food supply, given the tremendous challenges of climate change, food production, and food security [13].

## 2. Heirlooms and Sustainable Agriculture

Local landraces—defined as traditional cultivars developed over time after adapting to natural and cultural environments—or heirloom cultivars may perform better than modern-bred cultivars, particularly in marginal and climatic vulnerable sites. Heirlooms are known for their great trait diversity, e.g., for color, shape, size, growth, height, phenology, yield, and flavor. This wide diversity—which is the main feature capturing the attention of consumers seeking unique, nutritious, local food sources—also plays a key role in the risk management strategy of farmers if modern-bred cultivars are unsuitable for the local context [14]. Crop heterogeneity and diversity should therefore be included in a national asset strategy by rural development policy-makers, because such a valuable genetic endowment will be useful for further breeding. In this regard, Newton et al. [15] noted that landraces are sources of host-plant resistance and abiotic stress tolerance genes, as well as of phytonutrients with desired micronutrient concentrations that alleviate human aging-related and chronic diseases, and nutrient-use efficiency traits—which are very important for sustaining agriculture. Indeed, landraces show variation in their response to diverse stress-prone environments, and this heritage may be used as a genetic resource for breeding future crops [16]. For example, sweet potato heirlooms exhibit moderate to high host-plant resistance to soilborne insects, which provides interesting sources for developing new cultivars [17]; Hopi farmers in Arizona in the United States still plant 'Hopi blue maize' because it is adapted to drought and the short growing season and because of cultural significance [18]; native black and yellow maize landraces from Los Tuxtlas, Mexico are efficient phosphorus (P) colonizers and thus adapted to low soil P conditions [19]; farmers from northeast India still cultivate and maintain traditional rice cultivars because of their adaptation to harsh growing conditions [20–22]; heritage durum wheat cultivars are more tolerant to drought than modern cultivars [23]; and Spanish and Italian farmers in some regions still cultivate tomato landraces that are highly adapted to drought and salinity [24,25].

## 3. Genetic Enhancement Using Heirlooms and Further Seed Supply of Bred-Cultivars for Organic Farming

Crossbreeding—based on controlled crossing, population improvement, and family selection—is pursued to develop cultivars that may deliver greater elasticity for adapting to climate shifts, energy limitations, and low inputs in organic farming. The main traits of a successful organic cultivar outside of industrial agricultural production systems are host-plant resistance to pathogens (e.g., bacteria, fungi, oomycetes, phytoplasma, viroid, or viruses) and pests (birds, insects, and nematodes), ability to outcompete weeds, resource-use efficiency, abiotic stress and pollution tolerance, adaptability to a range of soil quality factors, responsiveness to low plant density, improved nutritional content, and satisfactory yield under low-input conditions. Moreover, cultivars may be bred under organic conditions, thus providing suitable germplasm for such farming systems along with the desired quality traits for consumers. For example, dry bean consumers may like to buy heirlooms with unique color patterns, which may be also sold at premium prices [26]. Swegarden et al. [27] further indicated that both yield stability analysis and economic incentives suggest that heirloom dry bean cultivars—despite having a 44% lower average grain yield than commercial checks—may allow for diversifying production, differentiation in the market, and more attractive economic returns for their small-scale organic growers.

Seed production begins with the developer of the new cultivar, who often retains the original breeder stock that may be further used as the "golden standard" for such a cultivar and as source for the foundation stock [28]. The next step is producing registered seed for distribution to licensees, who produce certified seed, which is the last stage of large-scale seed production. Organic farming standards ask further for organically produced seed. Certified organic seed should be grown only in certified organic soil using the same inputs as in organic farming, and packaged in a certified facility. Crop husbandry includes protecting soil fertility, using manure, rotating crops, conserving biodiversity and natural resources, sound plant health management, and recycling, whereas any practices leading to accumulation of heavy metals and other pollutants are forbidden.

## 4. Promoting Conservation of Heirloom Germplasm

### *4.1. Seed-Savers and Heritage Seedbanks*

Some studies have estimated that up to 75% of plant genetic diversity has been lost due to the rapid expansion of industrial agriculture and large-scale adoption of monoculture farming [29]. Many such studies have been based on a reduction in the number of cultivars of particular crops, and, as such, may be inaccurate estimates of the amount of actual plant genetic diversity present when both gene banks and cultivars are considered. However, it appears likely that the homogenization of agricultural environments around the world and the drive towards widely adapted uniform cultivars of a few major crop species have translated into reduced genetic diversity currently deployed in farmers' fields. In addition to a narrowing of diversity of crop germplasm, there are worrying reports of reductions in the global diversity of plant species. The Millennium Ecosystem Assessment Reports state that 60,000 to 100,000 species of plant are currently threatened with extinction [30]. It is apparent that some of these species play critical roles in agricultural and natural ecosystems, and serve as reservoirs of important genes that could play a role in crop breeding. Hence, this reduction in plant biodiversity is a significant global concern.

One traditional practice that may improve the current state of crop genetic diversity is seed-saving. Practiced since the beginnings of agriculture itself, the simple act of saving and replanting seed from a crop was an integral part of food production in many parts of the world until the 20th century.

The development of an efficient and wide-reaching global seed industry, the convenience and quality enhancement of purchasing seed each year, and the appearance of technologies such as $F_1$ hybrids and intellectual property rights have all played a role in reducing the practice of seed-saving. From the point of view of crop genetic diversity, revitalizing the practice of seed-saving may, however, be viewed as vital for the world's sustainable food production and nutritional security.

There are several seed-saving projects, in addition to 1700 ex situ gene banks worldwide, including the CGIAR gene banks and Svalbard Global Seed Vault [31], that are involved in collecting and maintaining heirloom cultivars across the globe to preserve agricultural biodiversity. Arche Noah in Austria (https://www.arche-noah.at) and ASEED Europe, Camino Verde, Hawai'i Public Seed Initiative, Irish Seed Savers Association, Louisiana Native Plant Initiative, Man and the Biosphere Programme, Millenium Seed Bank Project, Native Seed/SEARCH, Navdanya, National Laboratory for Genetic Resources Preservation, New York City Native Plant Conservation Initiative, Australian Plantbank, Seed Savers Exchange, Seesave.org, Slow Food International, USC Canada, Vavilov Research Institute, and the World Vegetable Center house many traditional and rare cultivars of fruit, vegetable, flower, and grain crops [32]. Native American seed-savers are dedicated to on-farm preservation of their agrobiodiversity (heirlooms), but unwilling to share their seed heritage for preservation in ex situ gene banks (for fear of loss of ownership and access), as they believe that community-based in situ conservation will maintain local control and seed viability better than ex situ gene banks [31]. One excellent example of a collection of heirloom cultivars is held at the Heritage Seed Library (HSL) of Garden Organic, UK. It curates and maintains a collection of 800 heirlooms of carrot (*Daucus carota* L.), cucumber (*Cucumis sativus* L.), *Brassica oleracea* L. var. *acephala* (DC.) Metzq, faba bean (*Vicia faba* L.), pea (*Pisum sativum* L.), and lettuce (*Lactuca sativa* L.) [33]. Table 1 presents a list of a few websites providing further information on gene banks or seed-savers for heirloom cultivars.

**Table 1.** Some gene banks or seed-saver organizations providing heirloom cultivars or related information.

| Name | Website |
|---|---|
| AVRDC—The World Vegetable Center | https://avrdc.org/seed/ |
| Nature and Nurture Seeds | https://natureandnurtureseeds.com |
| Organic Seed Producer Directory | https://seedalliance.org/directory/ |
| Seed Savers Exchanges | https://www.seedsavers.org/mission |
| Sustainable Seed Company | https://sustainableseedco.com/# |
| The Kerr Center for Sustainable Agriculture | http://kerrcenter.com/publication/heirloom-vegetables-genetic-diversity-and-the-pursuit-of-food-security/ |

### *4.2. South and Southeast Asia*

Vrihi, the largest non-governmental in situ seed depository of traditional rice cultivars in eastern India, houses 610 rice landraces that withstand a much wider range of fluctuations in temperature and soil nutrient levels, as well as water stress, than modern rice cultivars. This collection includes numerous unique landraces, for example, the "Jugal," the doubled-grain rice, and "Sateen," the triple grain rice, long awn and erect flag leaf, or cultivars with distinct aroma, color, and taste. The Vrihi Seed Exchange Network has more than 6000 indigenous farmers who have received seeds from Vrihi and continue to cultivate and exchange seeds of these folk cultivars (synonymous to heirlooms) among themselves and to neighboring farmers [21]. At Basudha farm, located in the Rayagada district of Odisha, India, over 1400 folk rice cultivars and 30 other crops are grown every year, as a model of ecological agriculture and without any external inputs [www.cintdis.org/basudha]. The Philippines' Department of Agriculture, in collaboration with the International Rice Research Institute (IRRI, Philippines), has undertaken a project on raising productivity and enhancing the legacy of heirloom/traditional rice through empowering communities in unfavorable rice-based ecosystems in Philippines. This project has collected about 74 variants of 41 heirloom cultivars with distinct characteristics, with the sole aim to enhance productivity and livelihoods and conserve in situ, on-farm genetic resources [34].

### 4.3. USA

Native American seed-saving efforts are underway to preserve culturally significant seeds and knowledge to promote food sovereignty at the local or tribal level in the USA [31]. These consist of farmers and gardeners who share a common interest in keeping traditional and local crop diversity alive. They usually grow traditional crops and local cultivars of fruits and vegetables for cultural reasons, food preference, risk avoidance, local adaptation, and for niche market opportunities. Various groups, including the Indigenous Seed Keepers Network and Seedshed, have formed to foster the preservation and rematriation of heirloom strains of Native American crops, particularly of maize, bean, squash, tobacco, and sunflower. The Seed Savers Exchange (SSE), a non-profit heirloom seed gene bank based in Decorah, Iowa, saves and sells heirloom fruit, vegetable, and flower seeds in the USA. SSE has in its collection 24,000 rare fruit and vegetable cultivars [35]. This heirloom collection has immense variability, for example, its over 500 heirloom potato cultivars differ in tuber shape (round, oblong, and fingerling-shaped), skin (white, red, purple, and variegated), and flesh color (white, yellow, and purple), including varying skin and flesh color combinations, e.g., white skin–white flesh, white skin–yellow flesh, red skin–white flesh, red skin–yellow flesh, red skin–red or pink flesh [36]. Seed-saving efforts directed at heirloom cultivars may also be found in the southern/central Appalachia region, an area of relatively high crop biodiversity in the USA. In this region, a collection of 134 heirloom cultivars grown and saved by home-gardeners was documented, with beans being the most predominant and highly diverse group, followed by tomatoes, squash, corn, and potatoes. The decline of the farming population, combined with a lack of cultural continuance in family seed-saving traditions, however, threatens the ability of communities to maintain this crop biodiversity [7]. Culture and ethnicity also play an important role in preservation of heirloom cultivars [37–40].

### 4.4. Europe

There are numerous examples of seed-saver networks, for example, Réseau Semences Paysannes, Red de Semilla, and Rete Semi Rureli [41], involved in the organization of regional and local seed fairs, training workshops, participatory plant breeding activities, and transmission of farmers' knowledge about the selection and conservation of local cultivars [42]. The Réseau Semences Paysannes in France brings together all who are open to the development of peasant varieties. Peasant varieties, in this case, may be considered local cultivars originating from selection, identified as the collective heritage of the community and as heirlooms, and reproduced by all men and women who produce crops. The Red de Semillas is a technical, social, and political Spanish organization formed by the people that maintains agricultural biodiversity on peasant farms and on consumers' plates, whereas the Rete Semi Rureli has enacted regional laws to safeguard local agricultural biodiversity in Italy. The researchers associated with these networks are involved in the development of new cultivars shaped by history and participatorily bred with farmers. These cultivars are considered "peasant varieties" and are linked to the terroir of the plants [41].

### 4.5. Promoting Exchange of Heirloom Germplasm/Cultivars

Plant genetic resources are the basic raw materials for future genetic progress and an insurance against unforeseen threats to future agricultural production. Their use in crop improvement is one of the most sustainable ways to conserve valuable genetic resources. International and national policies, treaties, and agreements largely influence the use and distribution of plant genetic resources. Restrictive biodiversity laws in many countries prohibit or closely regulate the exchange of germplasm from other countries. This situation may, in the longer term, have a serious impact on the utilization of plant genetic diversity to cope with current and predicted challenges to agricultural production. Worldwide, over 7 million accessions (including some heirlooms) of plant genetic resources are preserved in over

1700 ex situ gene banks. However, obtaining seed samples from these gene banks is problematic, due to restrictions imposed by national governments. Ensuring conservation and sharing of such heritage germplasm and associated knowledge should be the priority. Adopting policies that foster consumer-oriented utilization and conservation of heritage germplasm could help ward off the dangers imposed by institutional and governmental restrictions on crop genetic resources [43].

## 5. Promoting Local Food Systems

Industrial agriculture, "Green Revolution" technologies, climate change, civil conflict, and change in market characteristics, including distance, have contributed to the erosion of farm-agrobiodiversity. The production and sale of heirloom cultivars are interdependent in local markets, suggesting that local food systems help preserve heritage diversity [44]. Modern food production systems based on Green Revolution technologies are neither sustainable nor nutritionally superior. Recent years have brought increased public awareness that the risk to onset of noncommunicable diseases (cancer, diabetes, heart diseases, and obesity) can be reduced by making changes in lifestyle and food habits [45,46]. Local food systems may be a critical component of lifestyle and of food habits that can contribute to improved public health.

Local food refers to food that is produced, sold, and consumed within a limited geographical area [47]. What drives consumers to buy locally produced food? People perceive that locally produced foods are fresher, taste better, are higher in minerals and vitamins, and safer than nonlocal food. The consumption of locally produced food is more environmentally sustainable than procuring food from global markets [44]. Attitudes towards supporting local agribusiness and preserving local heritage and tradition, keeping a connectedness with rural life, reducing one's carbon footprint (shorter transportation distance, minimizing the needs of packaging, processing, and refrigeration, among others), and protecting the environment for sustainable ecosystems also drive the public to consume locally produced foods [48–50]. Higher prices, accessibility, time constraints, and availability are, however, major barriers for consumption of local food [51,52]. Farmers' markets (FMs) refer to "markets where agricultural products are directly sold by producers to consumers through a common marketing channel" [53]. The "Buy local" initiative and "Buy local" movements in North America and western Europe have reinforced greater patronage at FMs and the belief of people that local food is fresher than food from farther away, and that buying local food benefits local farmers and the local economy as well as improving environmental sustainability [50,54].

## 6. Heirlooms' Nutritional, Sensory, and Culinary Characteristics

### *6.1. Pulses and Cereals*

The literature suggests significant genetic variation for physico-chemical, sensory, and culinary characteristics among heirloom cultivars. Unique seed coat colors and patterns as well as seed size and shape differentiate heirlooms from modern bean (*Phaseolus vulgaris*) cultivars. Heirloom beans have been shown to have relatively higher protein, total fiber, and soluble fiber, and greater in vitro antioxidant capacity than modern cultivars, and took less time to hydrate (4.33 to 5.07 h compared to 8.1 h for the modern cultivars) but had a similar cooking time (~1 h). A few heirlooms had high flavonoids and differed in softness even after cooking. "Hutterite Soup" and "Jacob's Cattle" showed lower firmness than "Kornis Purple" and "Tiger's Eye," which had textures similar to the control [55,56]. A common bean landrace, "Ganxet," is appreciated greatly for its culinary value in northeast Spain. The inbred lines representing the variability within Ganxet germplasm showed greater protein, less total dietary fiber, more digestible dietary fiber, a higher proportion of seed coat, more glucose, and less starch than control cultivars ("White Kidney," "Navy," "Faba Asturiana," and "Tolosa") [57]. Twenty-four heirloom beans from western Washington in the USA have been identified, with distinct appearances and great culinary value [58]. The Italian heirloom "Monachine" is known famously as

Pellegrini in honor of Seattle's culinary icon Angelo Pellegrini, who enjoyed this bean for decades, and it is now featured by a high-end regional restaurant because of its great culinary quality [59].

There is growing demand for maize with blue kernels because of its significant health benefits and unique culinary applications. Blue-kernel maize typically produces anthocyanins in the aleurone layer of the endosperm, whereas in purple maize, the anthocyanin is produced predominantly in the pericarp of the kernel [60]. The variation in total anthocyanin content among maize heirlooms ranged from 17.6 to 65.1 mg 100 g seed$^{-1}$, with an average of 49.6 mg 100 g$^{-1}$. Cyanidin and pelargonidin were the major components, and peonidin and succinyl 3-glucoside were the minor components. Heirlooms with blue kernels had higher anthocyanin than those with purple or red kernels. "Navajo Blue" and "Ohio Blue" displayed highest anthocyanin values, whereas "Santa Clara Blue" and "Flor del Rio" had highest oil and protein contents [61]. The variants of a pericarp-pigmented heirloom, "Apache Red Purple," showed greater variation in anthocyanin concentrations (210–6183 μg g$^{-1}$ pericarp), with some having greater proportions of either pelargonidin- or cyanidin/peonidin-derived anthocyanins [62].

Several Indian rice folk cultivars are either very nutritious or maintain their distinctive aroma and colors. "Kalanamak" (black-husked and short-grained rice) a non-basmati aromatic type famous for its distinct aroma, color, and taste, is a heritage rice from eastern India that has been in cultivation for the last 4000 years [63]. Unpolished brown rices such as "Bhadoi," "Kabiraj Sal," "Shatia," or "Agniban" are high in iron and antioxidants, whereas Shatia and "Kartiksal" are rich in fiber but low in carbohydrates [64]. Many of the traditional cultivars possess health-related properties. For example, "Pichha vari," "Karthigai samba," "Dudhsar," and "Bhejri" enhance milk production in lactating mothers; "Kelas" and "Bhutmoori" cure anemia; "Paramai-sal" improves child growth; "Nyavara" treats neurotic disorders; "Karhainy" alleviates paralysis; "Gudna" treats gastric ailments [22,65]; "Karanga" treats dysenteric complaints; "Bora" treats jaundice; "Pakheru," "Saraiphool," "Karia Gora," "Dani Gora," and "Punai Gora" are traditionally used as a tonic; and people consuming "Bhama," "Danigora," "Karhani," "Ramdi," "Muru," "Hindmauri," and "Punaigora" rices can work in their fields for a whole day without feeling hungry [65].

The white-seeded durum wheat landrace "Aybo" is highly preferred for use in holy communion and for making difo-dabo, and "Set-Akuri," "Arndeto," "Loko," "Kurkure," and "Mengesha" are known for their superior baking quality and used for making difo-dabo and injera. Difo-dabo is a traditional homemade bread prepared from flour by fermenting thick dough, and injera is a thin, flat, and spongy pancake-like product from fermented dough baked using traditional mitad [66]. Farmers in northeast Ethiopia maintain several landraces for specific end-uses; for example, "Nechita" is used for preparing thick porridge (genfo) and shorba for a semi-fluid drink from cracked grains. "Tikur gebs" is used for a beverage. "Temej" is used for kolo (roasted grain), and "Enat gebs," "Sene gebs," and "Meher gebs" are used for injera [67].

### *6.2. Vegetables*

*Cucurbita* (pumpkins and squash), either young or mature, entered Italian kitchens by the middle of the 16th century. A greater proportion of colored exocarp and firm mesocarp in long and narrow cucurbits, compared to round-fruited, provided better eating quality if the young fruits were consumed whole. This culinary use of long-fruited cucurbits has been the driving force behind the several independent evolutions of long-fruitedness in *C. pepo* [68]. Some of the oldest Italian squash heirloom cultivars are "Costata Romanesca," which dates to 1590, "Cocozelle," dating back to the early 19th century, and "Tondo di Nizza," from the mid-19th century [68].

The Puglia region in Italy possesses a vast pool of local heirloom vegetable cultivars (https://drive.google.com/file/d/1uVemsY6zE4zt-ivPLEUaQjar7zgDb-ZI/view?usp=sharing) that are maintained and cultivated by farmers. Tomato landraces in the Puglia region of Italy are maintained by farmers by repeated selection generation after generation for desired organoleptic quality. Shelf-life after harvest is among the most sought-after quality traits in tomato. "Regina," a landrace adapted to the coastal saline soils of central Puglia, is known for its unique qualitative profile, characterized by high concentrations of tocopherols, lycopene, and ascorbic acid, and long shelf-life [69]. “Corbarino” and “Lucariello” tomatoes are prized highly by consumers in Italy for the superior quality of their fruits and shelf-life. Corbarino produces an intense red color and has high levels of soluble and total solids, whereas Lucariello possesses a heart-shaped fruit with a pronounced pointed apex of less intense red and a thick cuticle [25].

A large number of heirloom cultivars of melons and watermelons have been described in a book titled “Melons for the Passionate Grower” [70], squash and pumpkins in a book titled “The Compleat Squash” [71], and tomatoes in a book titled “The Heirloom Tomato” [72], which may be consulted for further details.

Heirloom tomatoes from North America show abundant diversity in fruit weight (5–150 g), shape (elongated, flattened, rounded, heart-shaped, pyriform), color (white ivory, yellow, orange, red, black), firmness, and brightness, as well as chemical quality characteristics TSS (total soluble solids), TA (titratable acidity), TSS:TA ratio, flavor intensity, and ascorbic acid [73]. “Criollo” tomatoes from the Andean valley in Argentina are valued highly for their flavor and taste [74]. A few populations of heirloom tomatoes from eastern Spain showed high mean values for ascorbic acid (308 mg $kg^{-1}$ fruit weight, fw), lycopene (130 mg $kg^{-1}$ fw), β-carotene (30 mg $kg^{-1}$ fw), and total phenolics (89 mg caffeic acid 100 $g^{-1}$ fw), and may therefore be best suited as sources of functional compounds [75].

A multicolored landrace of carrot, “yellow-purple Polignano,” included in the “slow food” list of traditional products (https://www.fondazioneslowfood.com/en/what-we-do/slow-food-presidia/), has been in cultivation for decades by small farmers in Italy’s Puglia region. This landrace is appreciated greatly for its multicolored roots (outer core ranges from yellow or deep orange to dark purple, with an inner core of pale yellow to light green), special taste, tenderness, crispness, flavor, and fragrance. On average, it has a 22% lower total glucose, fructose, and sucrose content, but has a similar sweetness to a commercial cultivar. Fructose is the major contributor to its distinctive flavor as well as to its glycemic index. The purple variants of this cultivar showed high levels of antioxidant activity, total phenols, carotenoids, and β-carotene [69,76]. Another colored race from the Apulia region of southern Italy, “Taggiano” (or Saint Ippazio), possesses an outer and inner core with purple and yellow-orange color, respectively. This heirloom is known for the popular cult of the Saint Ippazio; i.e., protection from Saint Ippazio against hernias or male impotency. It has high levels of bioactive compounds and antioxidant capacity compared to orange-rooted cultivars [77].

## 7. Assessing Diversity among Heirloom Germplasm

Assessment of genetic diversity and population structure of heirloom cultivars will be of great help in identification of diverse heirloom germplasm with beneficial traits for breeding or farming. For example, amplified fragment length polymorphism (AFLP) analysis of 171 heirlooms from the Heritage Seed Library (HSL) of Garden Organic revealed 1.5- to 2-fold differences in heterozygosity within carrot, cucumber, and *Brassica* spp. (*Brassica oleracea* var. acephala (DC.)) accessions, as well as 3.6- to 9-fold differences within faba bean, pea, and lettuce accessions [33]. Heirloom beans from southern Italy exhibited significant diversity in seed shape (cuboid, kidney, oval, round, truncate), seed coat pattern (absent, bicolor, pattern around hilum, speckled, spotted bicolor, stripped), seed color (black, brown, grey, vine, violet, white), seed weight (21–74 g 100 seed), and phaseolin (C, T, S) [78]. Phaseolin is a storage grain protein encoded by the *phas* gene in common bean. The three distinct forms of phaseolins in common bean are S-, T-, and C-types, identified respectively from “Sanilac” (S), “Tendergreen” (T), and “Contender” (C) cultivars [78]. “Badda,” a round, large-seeded bean with a partially colored seed coat, has been in cultivation for more than two centuries by Sicilian farmers. Over the centuries of its cultivation, this landrace has diverged into two easily distinguished morphotypes, i.e., “Badda bianco” (white badda) and “Badda nero” (black badda). The Badda morphotypes can be grouped into three distinct clusters, namely, Badda bianco accessions in one cluster and those of Badda nero in two separate, well-distinguished clusters [79].

Microsatellite-based genetic diversity analysis of over 100 rice heirlooms from Northeast India detected three genetically distinct groups. Most *joha* rice accessions from Assam and *tai* rices from Mizoram and Sikkim were in cluster 1, whereas *chakhao* rices from Manipur were grouped in cluster 2, and aromatic accessions from Nagaland in cluster 3. Pairwise FST between three clusters varied from 0.223 to 0.453 [80]. FST is a fixation index, a measure of genetic distance, which ranges from 0 to 1, where 0 means complete sharing of genetic material and 1 means the populations are genetically distinct (i.e., no sharing of alleles).

"Candy Roaster" heirloom squash fruits differ in size (10–250+ lbs), shape (round, cylindrical, teardrop, blocky), and color (pink, tan, green, blue, gray, or orange), yet most have fine-textured orange flesh [81], whereas variants of "Cappello da prete," another squash heirloom of the 19th century, still grown in the Po Valley of northern Italy, differ significantly in fruit weight, pulp thickness, rind thickness, peduncle diameter, and seed weight [82]. Using highly polymorphic simple sequence repeats (SSRs) on a collection of 85 winter squash and pumpkin (*Cucurbita maxima* Duchesne) accessions, Kaźmińka et al. [83] noted two distinct clusters, with cluster 1 possessing modern breeding lines and cultivars characterized by small fruits (<5 kg) and bushy or vine growth habit, while cluster 2 contained old cultivars from central and eastern Europe, together with breeding lines and cultivars characterized by large fruits and vine growth habit. The Australian and New Zealand cultivars had longer fruit shelf-life. Thus, they concluded that old cultivars were an interesting source of genetic variation for breeding novel hybrids.

Italian tomato landraces Corbarino and Lucariello are known for adaptation to water deficit, prolonged fruit shelf-life, and good fruit quality. Whole-genome sequencing revealed 43,054 and 44,579 gene loci annotated in Corbarino and Lucariello. Both genomes exhibited novel regions with similarity to tomato wild species *Solanum pimpinellifolium* and *S. pennellii*, and single nucleotide polymorphisms (SNPs) or candidate genes associated with fruit quality, shelf-life, and stress tolerance [25]. Heirloom tomatoes, e.g., Criollo from an Andean valley in Argentina, are known for their excellent organoleptic quality, especially flavor and aroma. Aroma and sourness in Criollo fruit correlate with citrate and several volatile organic compounds, such as α-terpeneol, *p*-menth-1-en-9-al, linalool, and 3,6-dimethyl-2,3,3a,4,5,7a-hexahydrobenzofuran (DMHEX), which is a novel volatile compound discovered in this heirloom cultivar [74]. The fruit shape among Italian tomato landraces ranges from flattened or ribbed through pear or oxheart to round or elongated types. Although round or elongated types are rich in glycoalkaloids, the flattened types are rich in phenolic compounds [84]. North American heirloom tomatoes have been found to vary in fruit color (white, yellow, orange, red, or black), shape (elongated, flattened, heart-shaped, pyriform, or rounded), weight (4.2 to 265 g), firmness, total soluble solids (TSS) content, titrable acidity (TA), TSS:TA ratio, flavor intensity, and ascorbic acid concentration (Figure 1) [73]. Clearly, heirloom cultivars differ across crops, as noted above, maintain unique diversity, and can serve as a valuable resource for gardeners, farmers, and plant breeders.

The colocynth or desert watermelon (*Citrullus colocynthis*, CC) is a perennial watermelon adapted to desert soils throughout northern Africa, the Middle East, and southwestern Asia, and possesses genes for enhancing disease and pest resistance in cultivated watermelon (*Citrullus lanatus* var. *lanatus*, CLL) cultivars. A study on genetic diversity and relationships among CC, CLL, citron melon (*C. lanatus* ssp. *lanatus* var. *citroides*, CLC), and desert perennial (*C. ecirrhous*, CE) accessions revealed five groups corresponding to their geographic origins, and an additional group with admixture. Group 1 contained accessions from northern Africa that were distinguished by two subgroups. Group 2 and 3 included accessions mainly from the Middle East. The fourth and fifth groups were represented by single CC accessions, collected in Iran and Egypt, respectively. Each of these groups contained unique alleles, but also shared alleles with CLL, CLC, or CE, implying evolution from a common ancestor [85].

**Figure 1.** Diversity in fruit, root, and tuber size and color of heirloom cultivars of capsicum, carrot, potato, and tomato. Photo credit: University of Wisconsin—Madison College of Agricultural and Life Sciences.

## 8. Retaining Culinary and Nutritional Traits and Improving Heirloom Productivity

There is wide variation in productivity among heirloom cultivars when grown in organic farming systems. A few heirloom cultivars can compete with modern cultivars in organic systems, but almost no heirlooms can compete with modern cultivars under intensive production systems [26,27,86–88]. However, heirloom cultivars possess great diversity in fruit and seed size, shape, and appearance. They may often be superior in culinary and nutritional quality, and represent a rich source of many health-promoting compounds. Thus, improving the productivity while retaining the culinary, nutritional, and health-promoting compounds of heirloom cultivars is a great challenge for future plant breeding efforts [89]. For example, the heritage rice from eastern India Kalanamak is a tall, low-yielding, black-husked, short-grained rice superior to "Basmati" in aroma and taste. Its acreage has gone down (from 50,000 to almost zero) over years of cultivation due to its low grain yield. A systematic attempt was made to collect and evaluate variants of Kalanamak, collected from farmers, and to identify accessions as most aromatic and true to perceived Kalanamak quality. Using pure line selection, UPCAR-KN-1-5-1-1 was released as "Kalanamak 3" (KN3) for cultivation in eastern Uttar Pradesh, India. Subsequently, several semi-dwarf breeding lines, developed through hybridization or induced mutation, outyielded KN3 by 40% [63]. A first semi-dwarf, non-black husk cultivar, "Bauna Kalanamak 102," with comparable cooking quality and aroma to "KN3," has been released for cultivation in eastern Uttar Pradesh [90].

Spaniards highly appreciate the Ganxet bean, which is a landrace adopted on the Iberian Peninsula due to its culinary values, i.e., seed coat tenderness and buttery texture. Over the years of its cultivation, the original Ganxet bean became contaminated, possibly due to cross-hybridization with other beans. Several variants (inbred lines) derived from the Ganxet populations were evaluated against commercial cultivars. These lines showed greater variability in protein content, total dietary fiber, digestible dietary fiber, seed coat, glucose, and starch contents than commercial cultivars. An inbred line, "L67," had many favorable characteristics (greater protein, less total digestible fiber, more digestible dietary fiber, a higher proportion of seed coat, more glucose, and less starch than commercial cultivars) and resulted in commercialization as true to the original Ganxet [64]. "Caparrona" is another heirloom bean that was grown largely by farmers in Monzón, Italy. The increasing modernization of agriculture at the end of 20th century resulted in its replacement by modern cultivars. Today, only a few local growers continue producing Caparrona beans, and mainly for family use. A systematic effort was made to recover this landrace from extinction. Seed samples from growers were grown, and two progenies true to Caparrona types in morphology, chemical composition, and agronomic performance were identified for commercializing Caparrona beans as a gourmet product by a local producers' association [91].

A major seed company, Seminis Vegetable Seeds, has released a multiple-disease-resistant heirloom-type tomato hybrid, "Purple Boy," with great taste and unique appearance (purple), which are often the characteristics of heirloom cultivars [http://www.hortibiz.com/item/news/seminis--releases--first--purple--tomato--hybrid/].

Intensive breeding of crops with a focus on yield and stress tolerance has led indirectly to a reduction in nutrition and flavor in certain cases [92,93]. Environmental and agricultural practices may also impact the intensity of flavor and aroma [94–96]. Flavor improvement is most difficult to achieve because of the difficulty of assessing the phenotype, as well as a lack of basic knowledge about the chemicals driving consumer preferences, the pathways of their synthesis, and genes regulating the output of these pathways [97]. Analyses of consumer preferences, together with accurate phenotyping and the use of modern genomics and analytical chemistry tools in breeding, as evidenced in case of melon, strawberry, and tomato, and participatory farmer–breeder–chef–consumer collaborations may facilitate development of a next generation of crops to meet the growing demands of safe and nutritionally enhanced foods with good flavor, color, aroma, and texture [88,98].

## 9. Farmer–Breeder–Chef–Consumer Partnerships Preserving Heirlooms' Unique Cultural and Culinary Significance

Within the last decade, several organizations have begun collaborative breeding efforts among farmers, chefs, culinary professionals, and plant breeders. One of these is the Culinary Breeding Network (https://www.culinarybreedingnetwork.com/), which is based at Oregon State University in Corvallis, Oregon in the USA. The goal of this organization is to build communities of plant breeders, seed growers, farmers, produce buyers, chefs, and other stakeholders to improve quality in vegetables and grains. The Culinary Breeding Network is interested in facilitating communication, collaboration, and participation in selection, so that cultivars with superior performance, flavor, texture, and culinary attributes may be developed. They are also trying to promote and expand the awareness of cultivars developed by independent and public sector plant breeders, and particularly those that have been selected for organic systems. Similar efforts are being made by another collaborative endeavor formed at the University of Wisconsin in Madison under the direction of Professor Julie Dawson (https://dawson.horticulture.wisc.edu/). This effort is known as the Seed to Kitchen Collaborative (https://dawson.horticulture.wisc.edu/chef-farmer-plant-breeder-collaboration/). In addition, a seed company known as Row 7 (https://www.row7seeds.com/) has recently been established to foster close cooperation between chefs, farmers, and plant breeders to heighten the focus on culinary trait breeding and the sale of cultivars with special culinary characteristics.

These efforts are not directed solely at heirloom cultivars that possess unique culinary attributes. Instead, these efforts are an attempt to capitalize on the connection between the cultivar and the user of that cultivar, which is celebrated with many heirlooms, but with cultivars that have been selected for modern cropping systems. Thus, the goal is to combine the satisfaction of heirloom cultivars with the modern traits needed for high-intensity farming, often in organic systems.

Part of the impetus for these efforts is the realization that many plant breeders must necessarily focus their efforts on commodity markets. In so doing, they often need to place greater emphasis on traits such as postharvest storability, harvestable yield, and host-plant resistance to pathogens. There is little question that such traits are of great importance for crop production. Breeders also recognized that improving specific culinary qualities was possible, but often may not be as high on the priority list as those traits that deliver the productivity the market requires. Many plant breeders therefore continued to focus on commodity traits and relegated specific culinary objectives to minor parts of their work.

Within the last 10 years, what were once small projects by plant breeders to modify culinary traits have blossomed into full-blown breeding programs. One of the primary thought leaders in this area is Chef Dan Barber, of Blue Hill and Blue Hill at Stone Barns in New York (https://www.bluehillfarm.com/team/dan-barber). Dan was among the first to realize that partnerships among chefs, farmers, and plant breeders were necessary to bring a focus on culinary traits to cultivars that could be grown and enjoyed widely. His efforts with the seed company Row 7 are one of the best examples of how such partnerships have formed in recent years. The Culinary Breeding Network and Seed to Kitchen Collaborative are attempts to bring many professionals together to participate in the development and selection of new vegetable cultivars. As such, it represents a new form of participatory plant breeding that rapidly is gaining interest in many parts of the world.

The origin of the Culinary Breeding Network was in 2011, when Lane Selman, an agricultural researcher at Oregon State University (https://www.culinarybreedingnetwork.com/), observed chefs and plant breeders sharing knowledge during a taste test of nine different sweet pepper cultivars. At that time, Lane was involved in the management of vegetable trials for the Northern Organic Vegetable Improvement Collaborative (NOVIC; http://eorganic.info/novic/), a federally funded partnership that uses on-farm trials to identify cultivars of vegetables that will thrive in organic systems. Farmers were trying to find a replacement for a hybrid sweet pepper that was no longer being offered for sale in the seed industry. Among the sweet peppers trialed were several cultivars developed by Frank Morton, breeder and owner of Wild Garden Seed in Philomath, Oregon (https://www.wildgardenseed.com/). In the field, these plants stood out, and the participants in the trial began to discuss the various qualities of these peppers. This discussion was followed by more in-depth discussions among the various stakeholders who could be growing, cooking, eating, and producing seed of these peppers. A participatory network was thus born.

While plant breeders of horticultural crops often taste the breeding lines that they are developing, their evaluations typically lack the sort of analysis that may be common for chefs or other culinary professionals. For example, many plant breeders "bite test" their breeding materials in the field, rendering an opinion when comparing among lines, but often lacking in the sort of detailed observation that might be helpful in the culinary arts. When chefs and plant breeders finally started coming together in these efforts, the conversations that ensued were eye opening. Chefs often expressed interest in traits breeders had never considered, or typically would throw out. An expansion of the stakeholders involved in selection made for a much more robust selection process. Importantly, this sort of participatory breeding has a better chance of resulting in an adopted cultivar, given the involvement of many different stakeholders during cultivar development. Conversely, as culinary specialists come to appreciate the challenges and limitations of the plant breeding process, there is a much better overall understanding of what is possible for the future of our crops. Both the Culinary Breeding Network and the Seed to Kitchen Collaborative combine field trials with tasting events that allow for such conversations to occur.

The goal of the Seed to Kitchen Collaborative (SKC) is to connect farmers, plant breeders, and chefs to develop better cultivars for regional food systems in the Upper Midwest. The collaborative uses farmer focus groups and surveys to identify traits of interest, and flavor is consistently one of the top traits from these surveys. Currently, 80 farms are participating in this collaborative undertaking, and the majority of these farms use information gleaned from trials to find the cultivars that they use in their production systems. Another important aspect of the collaborative initiative is that it provides an opportunity for independent plant breeders and public sector plant breeders to trial their newest material. For many specialty crops, organized trailing programs do not exist; therefore, the collaborative provides a unique outlet for breeding programs.

Acorn squash is a very old cultivar group of *Cucurbita pepo* subsp. *texana*, characterized by its distinctive turbinate shape marked with ten alternating ridges and furrow. This cultivar group was developed by Native Americans of eastern North America by the late 15th and early 16th centuries [99]. It has fairly good quality. However, consumers often add sweeteners in its culinary preparations. Sensing this need, breeders in Israel developed a new hybrid cultivar of acorn squash called "Table Sugar," characterized by a bush growth habit and powdery mildew resistance, fruits with black-green exterior color, increased sweetness, chestnut flavor, and a solids content of 12–18%. The breeder teamed up with a seed producer, grower, supermarket chain, and chefs to introduce this new squash in Israel, and it was then proclaimed by the leading food magazine in that country to be "the finest-tasting pumpkin or winter squash ever developed" [100].

The Row 7 seed company began in 2017 as an effort to bring together breeders and chefs who want to make produce with better flavor and culinary characteristics. Founders of the Row 7 seed company, Chef Dan Barber, Professor Michael Mazourek of Cornell University, and Matthew Goldfarb of Fruition Seed Company, are filling a unique gap in the seed market. Their goal has been to promote and sell seeds for new vegetable and grain cultivars that might otherwise not have been sold by any seed company, because their primary characteristics could be their culinary attributes. Row 7's focus is to partner chefs and plant breeders, with the aim of creating new cultivars that will bring a focus on flavor to what may have otherwise been commodity crops [101].

Chefs have brought very useful and interesting perspectives to vegetable breeding efforts in Oregon and Wisconsin in recent years [102]. Chefs readily admit that the food that they prepare is only as good as the ingredients that they use, so cultivars with improved qualities will make their job easier and more satisfying. Sometimes, consumers and chefs can make an impact on cultivar development. Several examples described by Beans [102] include a new tomato cultivar developed by a cross between a modern breeding line, and an heirloom that was identified after a taste panel involving 100 consumers. A squash was developed by a plant breeder after extensive dialogue between himself and a chef, who trialed the product in restaurants during its development. Such collaborative breeding efforts widen the scope of traditional plant breeding, and likely forecast more consumer-friendly cultivars with enhanced culinary qualities.

## 10. Outlook

Heirlooms often embody particular shapes, colors, textures, flavors, and productivity traits for which they have come to be known and sought by farmers and consumers. They are recognized and prized for their specific qualities that have lent uniqueness to the cuisines of many of the world's cultures. Thus, the wealth of genetic variability encoded in heirloom cultivars of our crops is one of the treasures of our shared global food system; however, this treasure is not always freely shared, due to restrictions on the sharing and importation of germplasm.

As modern cultivars and the global seed industry have rapidly replaced heirlooms and the practice of seed-saving, this unique genetic heritage is, however, in danger of being lost. In recent decades, as our agricultural systems have become even more industrialized, many scientists have come to recognize that the genetic diversity of heirloom cultivars is of even greater importance for our shared food future. Modern crop breeding has improved agricultural productivity, but has simultaneously reduced genetic diversity in our major crops. As our farming systems become more industrialized and our climate becomes more erratic, enhancing, rather than shrinking, our crop genetic diversity will be critical for feeding the growing population of the world. Recent efforts to characterize, preserve, and enhance heirlooms abound, bringing these unique types to the forefront of many modern breeding efforts. Participatory breeding approaches with farmers, breeders, and chefs are but one example of modern approaches to expanding the diversity found in heirlooms into modern germplasm pools. Recently, molecular research has found markers associated with useful variants in heirloom cultivars that may be further used to introgress such traits into modern cultivars.

Heirloom cultivars also are closely associated with organic and sustainable farming systems, and typically do much better in such conditions than in modern, industrialized farming systems. As sustainable farming systems gain popularity in the developed world, the genetic diversity present in heirloom cultivars may become even more important. However, we realize that modern farming systems will continue to dominate many sectors of world agriculture. One of the most important breeding objectives going forward will therefore be to improve the productivity of heirloom types while retaining their unique qualities.

A number of groups have expanded their efforts to preserve traditional heirloom cultivars that have been important cultural touchstones for different ethnic groups around the world. One such example is the recent attempts to preserve, maintain, and repatriate germplasm of American crops domesticated and bred by Native American tribes. These efforts are closely tied to food sovereignty movements, which seek to bring particular heirloom types of staple food crops back under the control of the people who developed them. In such cases, heirloom cultivars represent a vital link to the past, as well as a critical bridge to the future. One of the most useful activities for the promotion of heirlooms would be documentation of these unique resources in text and photograph for the benefit of future generations.

One of the hallmarks of modern agriculture is the existence of high-performing cultivars that are bred for wide-area adaptation and productivity. These cultivars play a key role in feeding the world's growing population, but the narrowing genetic base of modern cultivars may make efforts to increase food production more difficult. Many decades ago, heirloom cultivars appeared to be relics of an earlier age. However, a renewed interest in heirloom cultivars has helped foster the sense that they may play an important role in future crop breeding efforts. New market channels have emerged for heirlooms and have re-energized this unique repository of crop germplasm. As they possess unique flavors, colors, texture, stress tolerances, and forms, heirlooms may represent an important collection of traits that can be of immediate value in crop production and as a source of breeding germplasm for future cultivars. The goal of this review has been to document some example of the unique characteristics of heirlooms, with the hope of further encouraging breeders to identify their useful exotic traits and introgress these traits into breeding programs aimed at developing high-quality, consumer-oriented cultivars.

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## References

1. Votava, E.J.; Bosland, P.W. Culivar by any other name: Genetic variability in heirloom bell pepper California Wonder. *HortScience* **2002**, *37*, 1100–1102. [CrossRef]
2. Kingsbury, N. *Hybrid: The History and Science of Plant Breeding*, 1st ed.; The University of Chicago Press: Chicago, IL, USA, 2009; pp. 1–493.
3. Wattnem, T. Seed laws, certification and standardization: Outlawing informal seed systems in the Global South. *J. Peasant Stud.* **2016**, *43*, 850–867. [CrossRef]
4. Jordan, J.A. The heirloom tomato as cultural object: Investigating taste and space. *Eur. Soc. Rural. Soc.* **2007**, *47*, 20–41. [CrossRef]
5. Tracy, W.F. Sweet corn. In *Specialty Corns*, 2nd ed.; Hallauer, A.R., Ed.; CRC Press: Boca Raton, FL, USA, 2001; pp. 155–197.
6. Navazio, J. *The Organic Seed Grower*; Chelsea Green Publishing: White River Junction, VT, USA, 2012; p. 388.

7. Veteto, J.R. The history and survival of traditional heirloom vegetable varieties in the southern Appalachian Mountains of western North Carolina. *Agric. Hum. Values* **2008**, *25*, 121–134. [CrossRef]
8. Rivard, C.L.; Louws, F.J. Grafting to manage soilborne diseases in heirloom tomato production. *HortScience* **2008**, *43*, 2104–2111. [CrossRef]
9. Barker, A.V.; Eaton, T.E.; Meagy, M.J.; Jahanzad, E.; Bryson, G.M. Variation of mineral nutrient contents of modern and heirloom cultivars of cabbage in different regimes of soil fertility. *J. Plant Nutr.* **2017**, *40*, 1–8. [CrossRef]
10. Flores, P.; Sánchez, E.; Fenoll, J.; Hellín, P. Genotypic variability of carotenoids in traditional tomato cultivars. *Food Res. Int.* **2017**, *100*, 510–516. [CrossRef] [PubMed]
11. Van Der Knaap, E.; Tanksley, S.D. The making of a bell pepper-shaped tomato fruit: Identification of loci controlling fruit morphology in Yellow Stuffer tomato. *Theor. Appl. Genet.* **2003**, *107*, 139–147. [CrossRef] [PubMed]
12. Fandika, I.R.; Kemp, P.D.; Millner, J.P.; Horne, D.; Roskruge, N. Irrigation and nitrogen effects on tuber yield and water use efficiency of heritage and modern potato cultivars. *Agric. Water Manag.* **2016**, *170*, 148–157. [CrossRef]
13. Petropoulos, S.A.; Barros, L.; Ferreira, I.C.F.R. Editorial: Rediscovering Local Landraces: Shaping Horticulture for the Future. *Front. Plant Sci.* **2019**, *10*. [CrossRef]
14. Coromaldi, M.; Pallante, G.; Savastano, S. Adoption of modern varieties, farmers' welfare and crop biodiversity: Evidence from Uganda. *Ecol. Econ.* **2015**, *119*, 346–358. [CrossRef]
15. Newton, A.C.; Akar, T.; Baresel, J.P.; Bebeli, P.J.; Bettencourt, E.; Bladenopoulos, K.V.; Czembor, J.H.; Fasoula, D.A.; Katsiotis, A.; Koutis, K.; et al. Cereal landraces for sustainable agriculture. A review. *Agron. Sust. Dev.* **2010**, *30*, 237–269. [CrossRef]
16. Dwivedi, S.L.; Cecarelli, S.; Blair, M.; Upadhyaya, H.D.; Are, A.K.; Ortiz, R. Landrace germplasm: A useful resource for improving yield and abiotic stress adaptation. *Trends Plant Sci.* **2016**, *21*, 31–42. [CrossRef] [PubMed]
17. Jackson, D.M.; Harrison, J.F. Insect resistance in traditional and heirloom sweetpotato varieties. *J. Econ. Entomol.* **2013**, *106*, 1456–1462. [CrossRef] [PubMed]
18. Cleveland, D.A.; Soleri, D.; Smith, S.E. Do folk crop varieties have a role in sustainable agriculture? *Bioscience* **2014**, *44*, 740–751. [CrossRef]
19. Sangabriel-Conde, W.; Negrete-Yankelevich, S.; Maldonado-Mendoza, I.E.; Trejo-Aguilar, D. Native maize landraces from Los Tuxtlas, Mexico show varying mycorrhizal dependency for P uptake. *Biol. Fertil. Soils* **2014**, *50*, 405–414. [CrossRef]
20. Das, T.; Das, A.K. Inventory of traditional rice varieties in farming systems of southern Assam: A case study. *Indian J. Tradit. Knowl.* **2014**, *13*, 157–163.
21. Deb, D. Valuing Folk Crop Varieties for Agroecology and Food Security. 2009. Available online: https://agrobiodiversityplatform.org/climatechange/2010/03/26/valuing-folk-crop-varieties-for-agroecology-and-food-security (accessed on 30 January 2019).
22. Deb, D. Folk Rice Varieties, Traditional Agricultural Knowledge and Food Security. 2012. Available online: https://www.researchgate.net/publication/233987520_Folk_Rice_Varieties_Traditional_Agricultural_Knowledge_and_Food_Security (accessed on 30 January 2019).
23. Slama, A.; Mallek-Maalej, E.; Ben Mohamed, H.; Rhim, T.; Radhouane, L. A return to the genetic heritage of durum wheat to cope with drought heightened by climate change. *PLoS ONE* **2018**, *13*, e0196873. [CrossRef] [PubMed]
24. Massaretto, I.L.; Albaladejo, I.; Purgatto, E.; Flores, F.B.; Plasencia, F.; Egea-Fernández, J.M.; Bolarin, M.C.; Egea, I. Recovering Tomato Landraces to Simultaneously Improve Fruit Yield and Nutritional Quality Against Salt Stress. *Front. Plant Sci.* **2018**, *9*, 1778. [CrossRef] [PubMed]
25. Tranchida-Lombardo, V.; Cigliano, R.A.; Anzae, A.; Landi, S.; Palombieri, S.; Colantuono, C.; Boston, H.; Termolino, P.; Aversano, R.; Batelli, G.; et al. Whole genome resequencing of two Italian tomato landraces reveals sequence variations in genes associated with stress tolerance, fruit quality and long shelf-life traits. *DNA Res.* **2018**, *25*, 149–160. [CrossRef]
26. Miles, C.; Atterberry, K.A.; Brouwer, B. Performance of heirloom dry bean varieties in organic production. *Agronomy* **2015**, *5*, 491–505. [CrossRef]

27. Swegarden, H.R.; Sheaffer, C.C.; Michaels, T.T. Yield stability of heirloom dry bean (*Phaseolus vulgaris* L.) cultivars in Midwest organic production. *HortScience* **2016**, *51*, 8–14. [CrossRef]
28. Adam, K.L. *Seed Production and Variety Development for Organic Systems*; ATTRA, the National Sustainable Agriculture Information Service; National Center for Appropriate Technology: Butte, MT, USA, 2005.
29. Jacques, P.J.; Jacques, J.R. Monocropping systems into ruin: The loss of fruit varieties and cultural diversity. *Sustainability* **2012**, *4*, 2970–2997. [CrossRef]
30. Millennium Ecosystem Assessment. *Ecosystems and Human Well-Being: Biodiversity Synthesis*; World Resources Institute: Washington, DC, USA, 2005.
31. Breen, S.D. Saving seeds: The Svalbard Global Seed Vault, Native American seed savers, and problems of property. *J. Agric. Food Syst. Commun. Dev.* **2014**, *5*, 39–52. [CrossRef]
32. Perroni, E. Twenty Initiatives Saving Seeds for Future Generations. 2017. Available online: https://foodtank.com/news/2017/07/seed-saving-initiatives/ (accessed on 30 January 2019).
33. Preston, J.M.; Ford-Lloyd, B.V.; Smith, L.M.J.; Sherman, R.; Munro, N.; Maxted, N. Genetic analysis of a heritage variety collection. *Plant Genet. Resour.* **2018**, *17*, 232–244. [CrossRef]
34. Manzanilla, D.; Lapitan, A.; Cope, A.; Vera Cruz, C. The heirloom rice story: A healthy fusion of science, culture and market. *CURE Matters* **2015**, *5*, 14–16.
35. Carolan, M.S. Saving seeds, saving culture: A case study of heritage seedbank. *Soc. Nat. Resour.* **2007**, *20*, 739–750. [CrossRef]
36. SSE. *Savers Potato Germplasm Collection: Using Phenotype and SSR Analysis to Characterize Heritage Solanum Spp Diversity Ex Situ*; Seed Savers Exchange: Decorah, IA, USA, 2014; Available online: https://pdfs.semanticscholar.org/f7de/6d9bdf9d4e91610e5a074544919856a40eea.pdf?_ga=2.242480258.1895016692.1550566917-687334884.1550566917 (accessed on 10 February 2019).
37. Hilgert, N.I.; Zamudio, F.; Furlan, V.; Cariola, L. The key role of cultural preservation in maize diversity conservation in the Argentine Yungas. *Evid. Based Complement. Altern. Med.* **2013**, *2013*, 1–10. [CrossRef]
38. Nazarea, V.D. Local Knowledge and Memory in Biodiversity Conservation. *Annu. Rev. Anthropol.* **2006**, *35*, 317–335. [CrossRef]
39. Perales, H.R.; Benz, B.F.; Brush, S.B. Maize diversity and ethnolinguistic diversity in Chipas, Mexico. *Proc. Natl. Acad. Sci. USA* **2005**, *102*, 949–954. [CrossRef]
40. Wang, Y.; Wang, Y.; Sun, X.; Caiji, Z.; Yang, J.; Cui, D.; Cao, G.; Ma, X.; Han, B.; Xue, D.; et al. Influence of ethnic traditional cultures on genetic diversity of rice landraces under on-farm conservation in southwest China. *J. Ethnobiol. Ethnomed.* **2016**, *12*, 51. [CrossRef] [PubMed]
41. Bocci, R.; Chable, V. Peasant seeds in Europe: Stakes and prospects. *J. Agric. Environ. Int. Dev.* **2009**, *103*, 81–93.
42. Da Via, E. Seed diversity, farmers' rights, and the politics of repeasantization. *Int. J. Sociol. Agric. Food* **2012**, *19*, 229–242.
43. Paris, H.S. Consumer-oriented exploitation and conservation of genetic resources of pumpkins and squash, Cucurbita. *Isr. J. Plant Sci.* **2018**, *65*, 202–221. [CrossRef]
44. Goland, C.; Bauer, S. When the apple falls close to the tree: Local food systems and the preservation of diversity. *Renew. Agric. Food Syst.* **2004**, *19*, 228–236. [CrossRef]
45. Arena, R.; Guazzi, M.; Lianov, L.; Whitsel, L.; Berra, K.; Lavie, C.J.; Kaminsky, L.; Williams, M.; Hivert, M.F.; Franklin, N.C.; et al. Healthy Lifestyle Interventions to Combat Noncommunicable Disease—A Novel Nonhierarchical Connectivity Model for Key Stakeholders: A Policy Statement from the American Heart Association, European Society of Cardiology, European Association for Cardiovascular Prevention and Rehabilitation, and American College of Preventive Medicine. *Eur. Heart J.* **2015**, *90*, 2097–2109.
46. Naicker, A.; Venter, C.S.; MacIntyre, U.E.; Ellis, S. Dietary quality and patterns and non-communicable disease risk of an Indian community in KwaZulu-Natal, South Africa. *J. Health Popul. Nutr.* **2015**, *33*, 12. [CrossRef] [PubMed]
47. Mirosa, M.; Lawson, R. Revealing the lifestyles of local food consumers. *Br. Food J.* **2012**, *114*, 816–825. [CrossRef]
48. Arsil, P.; Li, E.; Bruwer, J.; Lyons, G. Exploring consumer motivations towards buying local fresh food products: A mean-end approach. *Br. Food J.* **2014**, *116*, 1533–1549. [CrossRef]
49. Bianchi, C.; Mortimer, G. Drivers of local food consumption: A comparative study. *Br. Food J.* **2015**, *117*, 2282–2299. [CrossRef]

50. Dukeshire, S.; Garbes, R.; Kennedy, C.; Boudreau, A.; Osborne, T. Beliefs, attitudes, and propensity to buy locally produced food. *J. Agric. Food Syst. Commun. Dev.* **2011**, *1*, 19–29. [CrossRef]
51. Khan, F.; Prior, C. Evaluating the urban consumer with regard to sourcing local food: A heart or England study. *Int. J. Consum. Stud.* **2010**, *34*, 161–168. [CrossRef]
52. Tippins, M.J.; Rassuli, K.M.; Hollander, S.C. An assessment of direct farm-to-table food markets in the USA. *Int. J. Retail Distrib. Manag.* **2002**, *30*, 343–353. [CrossRef]
53. Ragland, E.; Tropp, D. *USDA National Farmer Market Manager Survey 2006*; Agricultural Marketing Service USDA: Washington, DC, USA, 2009. [CrossRef]
54. Giampietri, E.; Koemle, D.B.A.; Yu, X.; Finco, A. Consumers' Sense of Farmers' Markets: Tasting Sustainability or Just Purchasing Food? *Sustainability* **2016**, *8*, 1157. [CrossRef]
55. Garretson, L.; Marti, A. Pigmented Heirloom Beans: Nutritional and Cooking Quality Characteristics. *Cereal Chem. J.* **2017**, *94*, 363–368. [CrossRef]
56. Garretson, L.; Tyl, C.; Marti, A. Effect of Processing on Antioxidant Activity, Total Phenols, and Total Flavonoids of Pigmented Heirloom Beans. *J. Food Qual.* **2018**, *2018*, 1–6. [CrossRef]
57. Casañas, F.; Bosch, L.; Pujolá, M.; Sánchez, E.; Sorribas, X.; Baldi, M.; Nuez, F. Characteristics of a common bean landrace (Phaseolus vulgaris L.) of great culinary value and selection of a commercial breeding line. *J. Sci. Food Agric.* **1999**, *79*, 693–698.
58. Brouwer, B.; Winkler, L.; Atterberry, K.; Jones, S.; Miles, C. Exploring the role of local heirloom germplasm in expanding western Washington dry bean production. *Agroecol. Sustain. Food Syst.* **2016**, *40*, 319–332. [CrossRef]
59. Leson, N. The Monachine Bean is Truly a Pellegrini Family Heirloom, the Seattle Times. 2013. Available online: https://www.seattletimes.com/pacific-nw-magazine/the-monachine-bean-is-truly-a-pellegrini-family-heirloom/ (accessed on 30 October 2018).
60. Li, Q.; Somavat, P.; Singh, V.; Chatham, L.; Gonzalez de Mejia, E. A comparative study of anthocyanin distribution in purple and blue corn coproducts from three conventional fractionation processes. *Food Chem.* **2017**, *231*, 332–339. [CrossRef]
61. Nankar, A.; Holguin, F.M.; Scott, M.P.; Pratt, R.C. Grain and nutritional quality traits of southwestern U.S. blue maize landraces. *Cereal Chem. J.* **2017**, *94*, 950–955. [CrossRef]
62. Chatham, L.A.; West, L.; Berhow, M.A.; Vermillion, K.E.; Juvik, J.A. Unique flavanol-anthocyanin condensed forms in Apache Red purple corn. *J. Agric. Food Chem.* **2018**, *66*, 10844–10854. [CrossRef] [PubMed]
63. Chaudhary, R.C.; Mishra, S.B.; Yadav, S.K.; Ali, J. Extinction to distinction: Current status of Kalanamak, the heritage rice of eastern Uttar Pradesh and its likely role in farmers' prosperity. *LMA Conv. J.* **2012**, *8*, 7–14.
64. Basu, M. Reviving Traditional Rice Varieties in West Bengal. 2018. Available online: https://earthjournalism.net/stories/reviving-traditional-rice-varieties-in-west-bengal (accessed on 25 October 2018).
65. Rahman, S.; Sharma, M.P.; Sahai, S. Nutritional and medicinal values of some indigenous rice varieties. *Indian J. Tradit. Knowl.* **2006**, *5*, 454–458.
66. Tsegaye, B.; Berg, T. Utilization of durum wheat landraces in East Shewa, central Ethiopia: Are home uses as incentive for on-farm conservation? *Agric. Hum. Values* **2007**, *24*, 219–230. [CrossRef]
67. Shewayrga, H.; A Sopade, P. Ethnobotany, diverse food uses, claimed health benefits and implications on conservation of barley landraces in North Eastern Ethiopia highlands. *J. Ethnobiol. Ethnomed.* **2011**, *7*, 19. [CrossRef] [PubMed]
68. Lust, T.A.; Paris, H.S. Italian horticultural and culinary records of summer squash (Cucurbita pepo, Cucurbitaceae) and emergence of the zucchini in 19th-century Milan. *Ann. Bot.* **2016**, *118*, 53–69. [CrossRef] [PubMed]
69. Renna, M.; Serio, F.; Signore, A.; Santamaria, P. The yellow–purple Polignano carrot (Daucus carota L.): A multicoloured landrace from the Puglia region (Southern Italy) at risk of genetic erosion. *Genet. Resour. Crop Evol.* **2014**, *61*, 1611–1619. [CrossRef]
70. Goldman, A. *Melons: For the Passionate Grower*; Artison Books: New York, NY, USA, 2002.
71. Goldman, A. *The Compleat Squash: A Passionate Gowers's Guide to Pumpkins, Squash, and Gourds*; Artison Books: New York, NY, USA, 2004.
72. Goldman, A. *The Heirloom Tomato: From Garden to Table: Recipes, Portraits, and History of the World's Most Beautiful Fruit*; Bloomsbury: New York, NY, USA, 2008.

73. Rodríguez-Burruezo, S.; Prohens, J.; Roselló, J.; Nuez, F. "Heirloom" varieties as sources of variation for the improvement of fruit quality in greenhouse-grown tomatoes. *J. Hortic. Sci. Biotechnol.* **2005**, *80*, 453–460. [CrossRef]
74. D'Angelo, M.; Sance, M.; Asprelli, P.; Carrari, F.; Asis, R.; D'Sangelo, M.; Zanor, M.I.; Cortina, P.R.; Boggio, S.B.; Santiago, A.N.; et al. Contrasting metabolic profiles of tasty Andean varieties of tomato fruit in comparison with commercial ones. *J. Sci. Food Agric.* **2018**, *98*, 4128–4134. [CrossRef]
75. Cortés-Olmos, C.; Leiva-Brondo, M.; Roselló, J.; Raigón, M.D.; Cebolla-Cornejo, J. The role of traditional varieties of tomato as sources of functional compounds. *J. Sci. Food Agric.* **2014**, *94*, 2888–2904.
76. Cefola, M.; Pace, B.; Santamaria, P.; Signore, A.; Serio, F. Compositional analysis and antioxidant profile of yellow, orange and purple Polignano carrots. *Ital. J. Food Sci.* **2012**, *24*, 284–291.
77. Scarano, A.; Gerardi, C.; D'Amico, L.; Accogli, R.; Santino, A. Phytochemical analysis and antioxidant properties in colored Tiggiano carrots. *Agriculture* **2018**, *8*, 102. [CrossRef]
78. Piergiovanni, A.R.; Cerbino, D.; Brandi, M. The common bean populations from Basilicata (Southern Italy): An evaluation of their variation. *Genet. Resour. Crop Evol.* **2000**, *47*, 489–495. [CrossRef]
79. Loi, L.; Piergiovanni, A.R. Genetic diversity and seed quality of the 'Badda' common bean from Sicily (Italy). *Diversity* **2013**, *5*, 843–855. [CrossRef]
80. Roy, S.; Banerjee, A.; Mawkhleing, B.; Misra, A.K.; Pattanayak, A.; Harish, G.D.; Singh, S.K.; Ngachan, S.V.; Bansal, K.C. Genetic diversity and population structure in aromatic and quality rice (*Oryza sativa* L.) landraces from North-East India. *PLoS ONE* **2015**, *10*, e0129607. [CrossRef]
81. Neelamma, G.; Swamy, B.D.; Damodran, P. Phytochemical and pharmacological overview of Cucurbita maxima and future perspective as potential phytotherapeutic agent. *Eur. J. Pharm. Med. Res.* **2016**, *3*, 277–287.
82. Orsenigo, S.; Abeli, T.; Schiavi, M.; Cauzzi, P.; Guzzon, F.; Ardenghi, N.M.G.; Rossi, G.; Vagge, I. Morphological characterization of *Cucurbita maxima* Duchesne (*Cucurbitaceae)* landraces from the Po Valley (northern Italy). *Ital. J. Agron.* **2018**, *13*, 963. [CrossRef]
83. Kaźmińka, K.; Sobieszek, K.; Targońska-Karasek, M.; Korzeniewska, A.; Niemirowicz-Szczytt, K.; Bartoszewski, G. Genetic diversity assessment of a winter squash and pumpkin (*Cucurbita maxima* Duchesne) germplasm collection based on genomic Cucurbita-conserved SSR markers. *Sci. Hortic.* **2017**, *219*, 37–44. [CrossRef]
84. Baldina, S.; Picarella, M.E.; Troise, A.D.; Pucci, A.; Ruggieri, V.; Ferracane, R.; Barone, A.; Fogliano, V.; Mazzucato, A. Metabolite Profiling of Italian Tomato Landraces with Different Fruit Types. *Front. Plant Sci.* **2016**, *7*, 664. [CrossRef]
85. Levi, A.; Simmons, A.M.; Massey, L.; Coffey, J.; Wechter, W.P.; Jarret, R.L.; Tadmor, Y.; Nimmakayala, P.; Reddy, U.K. Genetic Diversity in the Desert Watermelon Citrullus colocynthis and its Relationship with Citrullus Species as Determined by High-frequency Oligonucleotides-targeting Active Gene Markers. *J. Am. Soc. Hortic. Sci.* **2017**, *142*, 47–56. [CrossRef]
86. Chapagain, T.; Riseman, A. Evaluation of heirloom and commercial cultivars of small grains under low input organic systems. *Am. J. Plant Sci.* **2012**, *3*, 655–669. [CrossRef]
87. Jankielsohn, A.; Miles, C. How do older wheat cultivars compare to modern wheat cultivars currently on the market in South Africa? *J. Hortic. Sci. Res.* **2017**, *1*, 42–47.
88. Nankar, A.; Grant, L.; Scott, P.; Pratt, R.C. Agronomic and kernel compositional traits of blue maize landraces from the southwestern United States. *Crop Sci.* **2016**, *56*, 2663–2674. [CrossRef]
89. Brouwer, B.O.; Murphy, K.M.; Jones, S.S. Plant breeding for local food systems: A contextual review of end-use selection for small grains and dry beans in western Washington. *Renew. Agric. Food Syst.* **2016**, *31*, 172–184. [CrossRef]
90. Kumar, S.; Mishra, S.B.; Chaudhary, R.C. Breeding Bauna Kalanamak 102 as new aromatic variety of heritage rice from Uttar Pradesh. *Int. J. Sci. Environ. Technol.* **2018**, *7*, 1690–1699.
91. Mallor, C.; Barberán, M.; Aibar, J. Recovery of a common bean landrace (*Phaseolus vulgaris* L.) for commercial purposes. *Front. Plant Sci.* **2018**, *9*, 1440. [CrossRef] [PubMed]
92. Marles, R.J. Mineral nutrient composition of vegetables, fruits and grains: The context of reports of apparent historical declines. *J. Food Compos. Anal.* **2017**, *56*, 93–103. [CrossRef]
93. White, P.J.; Broadley, M.R. Historical variation in the mineral composition of edible horticultural products. *J. Hortic. Sci. Biotechnol.* **2005**, *80*, 660–667. [CrossRef]

94. Dumas, Y.; Dadomo, M.; di Luca, G.; Grolier, P. Effects of environmental factors and agricultural techniques on antioxidant content of tomatoes. *J. Sci. Food Agric.* **2003**, *83*, 369–382. [CrossRef]
95. Cebolla-Cornejo, J.; Roselló, S.; Valcárcel, M.; Serrano, E.; Beltrán, J.; Nuez, F. Evaluation of genotype and environment effects on taste and aroma flavor components of Spanish fresh tomato varieties. *J. Agric. Food Chem.* **2011**, *59*, 2440–2450. [CrossRef]
96. Yanjie, X.; Yining, Y.; Shuhong, O.; Xiaolong, D.; Hui, S.; Shukun, J.; Shichen, S.; Jinsong, B. Factors affecting sensory quality of cooked japonica rice. *Rice Sci.* **2018**, *25*, 330–339. [CrossRef]
97. Klee, H.J.; Tieman, D.M. Genetic challenges of flavor improvement in tomato. *Trends Genet.* **2013**, *29*, 257–262. [CrossRef] [PubMed]
98. Folta, K.M.; Klee, H.J. Sensory sacrifices when we mass-produce mass produce. *Hortic. Res.* **2016**, *3*, 16032. [CrossRef] [PubMed]
99. Paris, H.S.; Nerson, H. Genes for intense pigmentation of squash. *J. Hered.* **1986**, *77*, 403–409. [CrossRef]
100. Paris, H.S.; Godinger, D. Sweet acorn squash, a new vegetable on the Israeli market. *Acta Hortic.* **2017**, *1127*, 451–456. [CrossRef]
101. Rao, T. Seeds Only a Plant Breeder Could Love, Until Now. *New York Times*. 27 February 2018. Available online: https://www.nytimes.com/2018/02/27/dining/row-7-seed-company-dan-barber.html (accessed on 20 January 2019).
102. Beans, C. Vegetable breeders turn to chefs for flavor boost. *Proc. Natl. Acad. Sci. USA* **2017**. [CrossRef] [PubMed]